

Discovery of *Anthophora onosmarum* Morawitz, 1876 in Europe (Hymenoptera, Apidae)

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Abstract

Anthophora onosmarum is a poorly known bee species described from the Caucasus (Georgia). New fieldwork has revealed that the species is present in Bulgaria and Greece, and is also widespread across Turkey, predominantly on the Anatolian plateau. New behavioural data shows that *A. onosmarum* is likely narrowly oligolectic on the plant genus *Onosma* (Boraginaceae), and is capable of buzzing flowers to release pollen. This finding illustrates the growing trend of overlooked bee species with more Caucasian, Anatolian, or even Middle Eastern distributions occurring in under-surveyed mountainous parts of the Southern Balkans.

Key Words

Balkans, oligolecty, *Onosma*, solitary bees

Introduction

Anthophora Latreille, 1803 is moderately large genus of bees, with around 430 species listed globally (Brooks 1988; Michener 2007; Ascher and Pickering 2024), and the genus is widely distributed in both the New (Nearctic and Neotropics) and Old Worlds (predominantly in the Palearctic and Afrotropical regions, with marginal occurrence in the Oriental region). Although it has a long history of study, our understanding of individual species, their distributions, and indeed the taxonomic status of the available names is hugely incomplete (e.g. Ras-mont and Wood 2024). Currently, 77 species are reported from Europe, making *Anthophora* the seventh largest genus of bees in this region (Ghisbain et al. 2023).

In this context, we take the opportunity to present new findings of the poorly studied species *Anthophora onosmarum* Morawitz, 1876 which was described from the Caucasus, from what is the modern day state of Georgia. To our knowledge, there has not been a single publication dealing with the ecology and distribution of this species

since its description, with only minimal treatment as to its subgeneric position (Brooks 1988) or cataloguing of its type material or publication date (Marikovskaya 2000; Ebmer 2021). We present its ecology and newly report the species from Europe for the first time.

Methods

Fieldwork in Bulgaria and Greece in May–June 2024 led to the discovery of *Anthophora onosmarum* as new for Europe. After associating the bee with *Onosma* sp. (Boraginaceae) in Bulgaria, during an 8-day trip in northern Greece in June 2024 in Western and Central Macedonia, we targeted *Onosma*-rich sites to find additional records of the bee. We visited approximately 20 sites, of which 10 were in dry, steppe-like slopes between 600–1000 m. *Onosma* plants were abundant at nine of these 10 sites, suggesting that this plant genus is widely distributed in hilly regions in northern Greece. Since *Onosma*-associated bees were of interest to us, we systematically surveyed

this plant genus whenever large stands were found. In agreement with Teppner (1995), *Osmia apicata* Smith, 1853 was the most common Boraginaceae-specialised bee during these searches; this species was present at a minimum of six of the 10 visited sites. Surprisingly, although we spent much time in sites with abundant *Onosma*, we observed *A. onosmarum* only at one site, where numerous specimens were present. Additionally, with the knowledge that *A. onosmarum* was present in Europe, searches of museum collections were able to uncover 23 additional previously unidentified specimens, clarifying the range of this species. All specimens were identified by TJW.

A DNA barcode was generated from a male specimen from Greece using the LepF/LepR primer, following standard protocols as mentioned in Praz et al. (2022). Field photographs were taken with a Canon EOS Rebel T6i with a Canon EF 100mm f/2.8L Macro IS USM lens. Specimen photographs were taken using an Olympus E-M1 Mark II with a 60 mm macro lens. Additional close-ups were taken with the addition of a Mitutoyo M Plan Apo 10X infinity corrected objective lens in combination with an Olympus M.Zuiko 2× teleconverter lens, a 10 mm Kenko DG extension tube, and a Meike MK-P-AF3B 10 mm extension tube. Photographs were stacked using Helicon Focus B (HeliconSoft, Ukraine) and plates were prepared in GNU Image Manipulation Program (GIMP) 2.10. Head length ratios were measured using photographs in GIMP, measuring from the top of the vertex to the anterior margin of the clypeus (head length) and between the outer margins of the compound eyes at their widest points (head width).

Abbreviations

IBER	Bulgarian Academy of Sciences, Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria
OÖLM	Oberösterreichisches Landesmuseum, Linz, Austria
PRUN	Research collection of Christophe Praz, University of Neuchâtel, Switzerland
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands
TJWC	Personal collection of T.J. Wood, Leiden, the Netherlands
ZISP	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia

Results

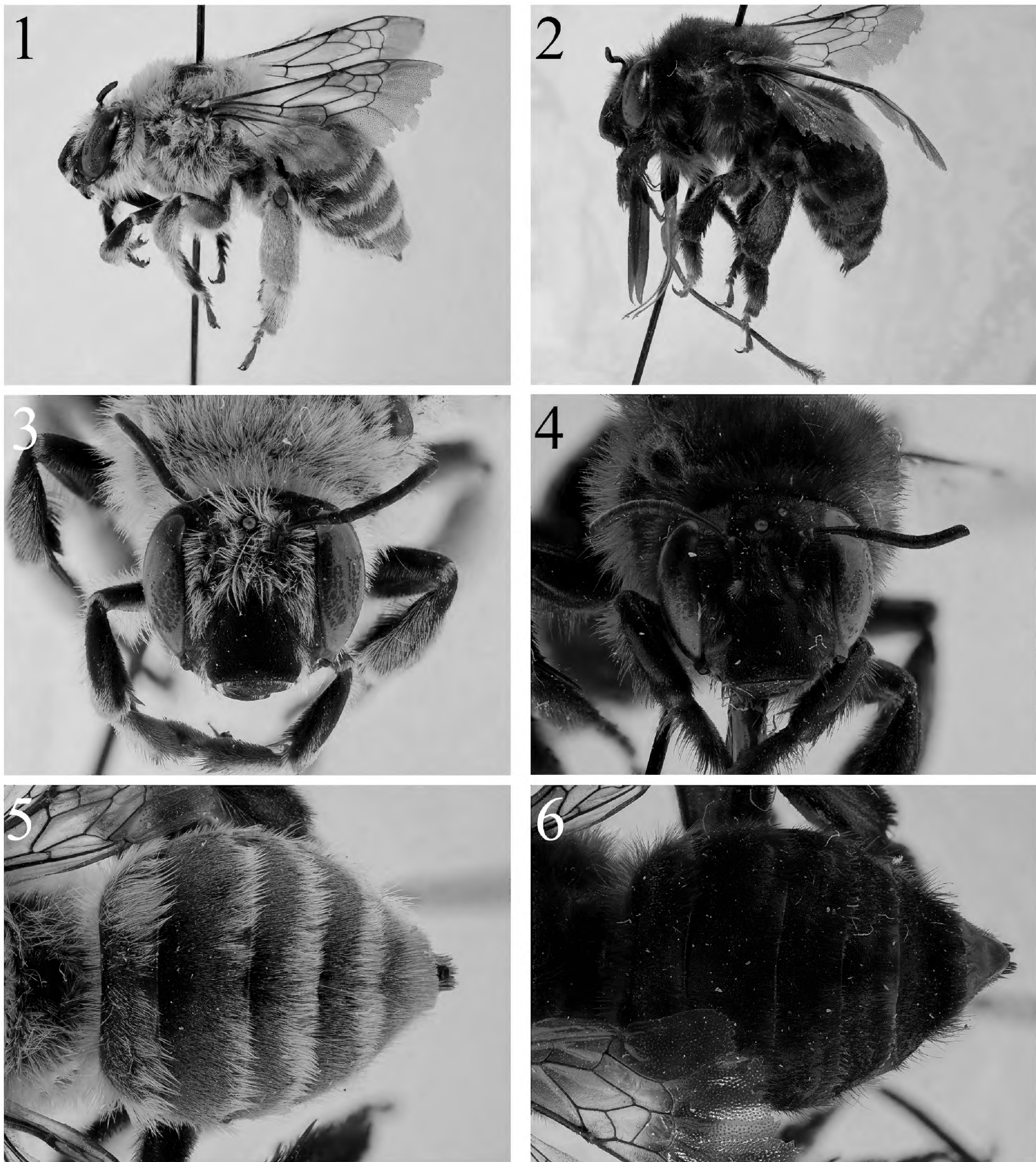
Anthophora (Paramegilla) onosmarum Morawitz, 1876

Anthophora onosmarum Morawitz, 1876: 15, ♀♂ [Azchur (presumably Azkur/ Atskuri, Georgia), ZISP, examined by photograph]

Material examined. **BULGARIA** • 1♂; Blagoevgrad, Gorno Spanchevo, 1.5 km E; 420 m a.s.l.; 22 May 2024;

T.J. Wood leg.; TJWC • 1♂; Stara Kresna; 20 Jun. 1987; Karas leg.; OÖLM (ex. collection B. Tkalců); **GREECE** • 1♂, 1♀; Western Macedonia, Kottas, 1.6 km E of Vatochori; 850 m a.s.l.; 13 Jun. 2024; T.J. Wood leg.; RMNH • 3♂, 1♀; Western Macedonia, Kottas, 1.6 km E of Vatochori; 850 m a.s.l.; 13 Jun. 2024; C. Praz leg.; PRUN; **IRAN** • 1♀; Zentralprovinz, 10 km nördlich Karadj [Karaj]; 1100 m a.s.l.; 23 May 1977; Holzschuh & Resel leg.; OÖLM; **TURKEY** • 1♂; 10 km W of Urgup [Ürgüp]; 15 Jun. 1998; Ma. Halada leg.; OÖLM • 2♂; 50 km S Kars, Pasli; 1 Jul. 1997; Ma. Halada leg.; OÖLM • 2♂; Bolu, S Karayokuş Gec Hocağ; 40.3503°N, 31.3003°E; 760 m a.s.l.; 19 Jun. 1986; E. Hüttinger leg.; OÖLM • 1♂, 1♀; Elazığ [Elâzığ]; Hazar-See; 1 Jun. 1978; M. Schwarz leg.; OÖLM • 1♂; Konya, 10 km S Karaman; 1100 m a.s.l.; 19 Jun. 1985; M. Schwarz leg.; OÖLM • 1♂; Konya: Karaman; 11 Jun. 1978; M. Schwarz leg.; OÖLM • 2♀; Madenşehir [Madenşehir]/Konya; 6 Jun. 1971; K. Warncke leg.; OÖLM • 2♀; Madenşehir [Madenşehir]/Konya; 22–23 Jun. 1984; K. Warncke leg.; OÖLM • 1♀; Malatya, 3 km SE of Kubbe Gecidi, st. 2641; 1700 m a.s.l.; 3 Jul. 2000; H. v. Oorschot, H. v. d. Brink, P. Oosterbroek leg.; RMNH; ZMA.INS.5144676 • 2♂; Maraş [Kahramanmaraş], Afsin [Afşin]; 8 Jun. 1985; OÖLM • 1♂; Meram, Konya; 14 Jun. 1968; K. Kudas leg.; OÖLM • 1♂; Nevşehir [Nevşehir], Urgup [Ürgüp]; 16 Jun. 1977; K. Warncke leg.; OÖLM • 1♂; Nevşehir, 10 km NE of Nevşehir; 1200 m a.s.l.; 5–7 Jul. 1982; H. v. Oorschot & H. v. d. Brink leg.; RMNH; ZMA.INS.5144674 • 1♂; Nordhand des östl. Hama dag, südl. Iğdir (Kars); 1300–1600 m a.s.l.; 27 Jun. 1971; Reinig leg.; OÖLM; • 1♂; Prov. Ankara, Bağlum [Bağlum Güzeyurt]; 1400 m a.s.l.; 13 Jul. 1961; J. Leinfest leg.; RMNH; ZMA.INS.5144675.

Diagnosis. There is currently no modern identification key for *Anthophora* that can be used in south-eastern Europe. The work of Friese (1897) is badly out of date due to the many taxonomic changes which have been made and must still be made in the Anthophorini. *Anthophora onosmarum* is included in this work (as *Podalirius* s. str.), but does not key out well as the mandibles can be partially yellow-marked, whereas Friese considered them to be entirely dark. Within the European fauna, *A. onosmarum* is best diagnosed due to the combination of its elongate head, in direct frontal view with the lower margin of the clypeus ventrally projecting below the lower margin of the compound eyes (Figs 3, 4), with the inner margins of the compound eyes slightly diverging ventrally (most strongly pronounced in the male sex, Fig. 8), head therefore relatively elongate, only 1.15–1.20 times wider than long (in comparison other *Anthophora* (*Paramegilla*) species with the head much wider than long, typically between 1.50–1.85 times wider than long), malar space slightly expanded but only subequal to length of antennal segment 4, clypeus bulging in profile view (extending as far in front of the compound eye as the diameter of the compound eye itself; Figs 1, 2), length of tongue very long, almost extending beyond tip of metasoma (Fig. 2), in female sex with metasoma covered with either adpressed pale yellow-orange

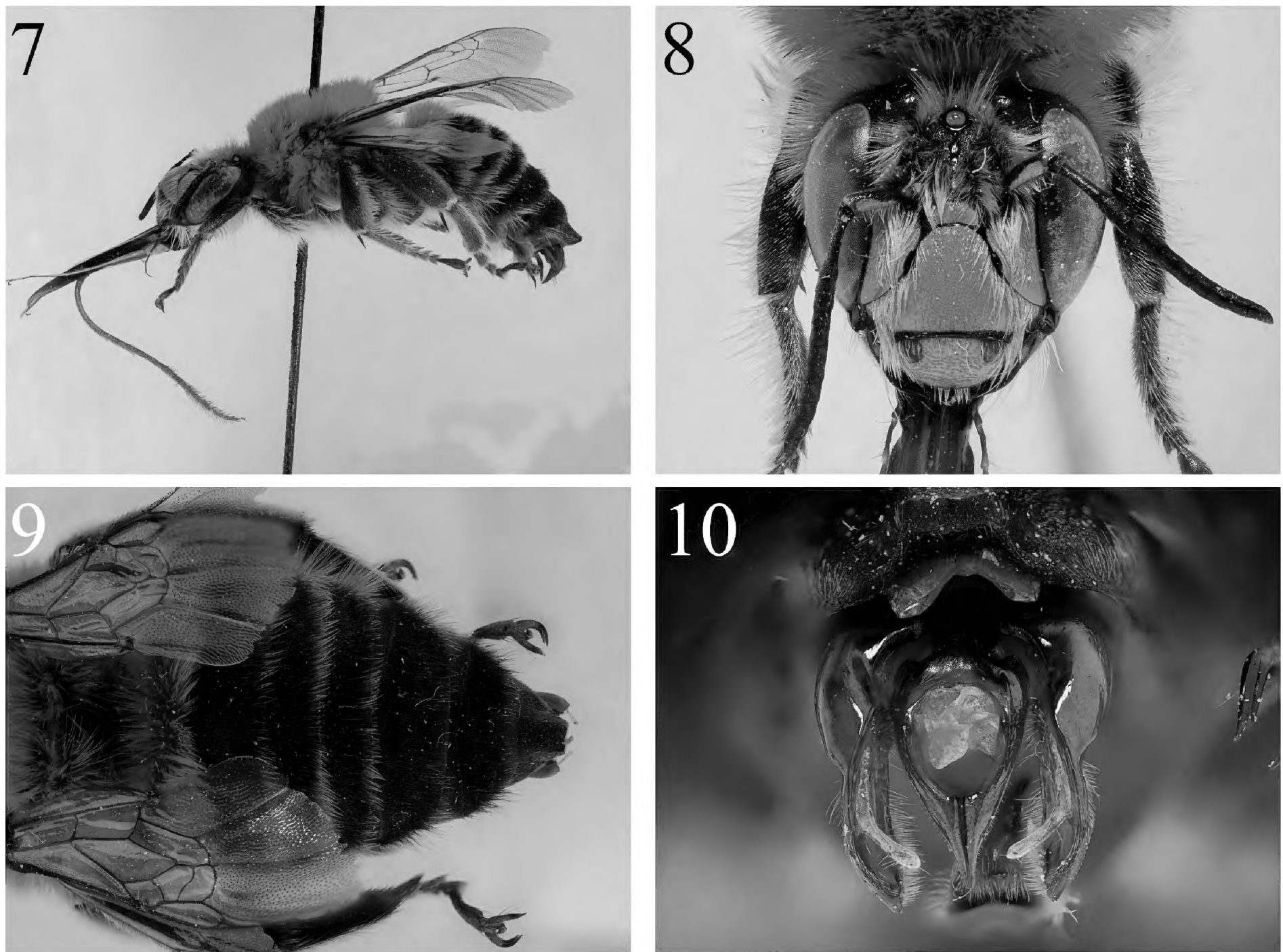


Figures 1–6. *Anthophora onosmarum* Morawitz, 1876 females, light (Turkey, Madenşehir; 23 Jun. 1984; K. Warncke leg.; OÖLM) and dark (Turkey, Madenşehir; 22 Jun. 1984; K. Warncke leg.; OÖLM) forms). **1.** Light form, profile; **2.** Dark form, profile; **3.** Light form, face, frontal view; **4.** Dark form, face, frontal view; **5.** Light form, metasoma, dorsal view; **6.** Dark form, metasoma, dorsal view.

pubescence (Fig. 5; intensity of colour depending on the age of the specimen) or adpressed black pubescence (Fig. 6), but if with black pubescence then without lateral white hairbands, male with extensive yellow markings on face, these covering the labrum, clypeus, lower paraocular areas to a level reaching the antennal insertions, ventral surface of antennal scape, and sometimes with a small dot on the mandibles (Fig. 8), mid legs without hair patches of fringes, hind basitarsi essentially unmodified (without

the presence of teeth) only slightly thickened apically, and genital capsule with gonocoxae produced into long apical projections which come to a curved apical point, with long, thin, and hyaline finger-like gonostyli (Fig. 10). A revised key to European *Anthophora* will hopefully be produced in the near future (TJW, in prep.).

Colour variation. A total of nine female specimens were examined, these showing two distinct colour morphs – four specimens showed black pubescence (Greece,



Figures 7–10. *Anthophora onosmarum* Morawitz, 1876 male (Bulgaria, Stara Kresna; 20 Jun. 1987; Karas leg.; OÖLM). **7.** Profile; **8.** Face, frontal view; **9.** Metasoma, dorsal view; **10.** Genital capsule, dorsal view.

central Turkey; Figs 1, 3, 5), and five showed yellow pubescence (central and eastern Turkey, Iran; Figs 2, 4, 6). There was a weak geographic gradient with darker individuals in the west and lighter individuals in the east, but on two occasions (Madenşehir, 6th June 1971 and 22–23rd June 1984) Klaus Warncke collected one black and one yellow female at the same place. The specimens illustrated in Figs 1–6 are from Madenşehir from the 22–23rd June 1984. Very little is known about colour variation in Anthophorine bees, and we make no decisive comments here, other than to say that for at least *A. onosmarum* this seems to represent simple variation, as it is not accompanied with structural differences. Morawitz (1876) described the female as being of the yellow form: “*Das Weibchen ist schwarz, das Gesicht, die Schläfen und die Brust weiss, das Hinterhaupt, die obere Fläche des Thorax und das erste Abdominalsegment sehr dicht fuchsroth behaart*” [The female is black, the face, the gena and the mesosoma has white hairs, the dorsal part of the thorax and the first metasomal segment dense, bright orange-red hairs]. In some *Andrena* species (Andrenidae), specimens from the Balkans are darker, for example *Andrena* (*Hoplendrena*) *clusia* ssp. *prilepensis* Warncke, 1973 (described from North Macedonia) which is almost completely melanic relative to the nominate subspecies which was described from Azerbaijan. This can also be seen

in *Eucera* (*Cubitalia*) *breviceps* (Friese, 1911) (Apidae) (Aubert et al. 2024a). In any case, male *A. onosmarum* appear to be much more consistent in terms of their colouration, with no melanic individuals observed so far. This would appear to fit the overall pattern of reduced colour variation in male anthophorines relative to females (e.g. Brooks 1983).

Genetics. We obtained a full-length (658 base pairs) DNA barcode from a male specimen (BOLD accession number HYMAA898-24; www.boldsystems.org); when submitted to the identification tool in the Bold Systems, the closest matches (87.4–89.5% similarity) were to *Anthophora* (*Paramegilla*) *balneorum* Lepeletier, 1841, *A.* (*Paramegilla*) *nigrovittata* Dours, 1872, and *A.* (*Dasymegilla*) *quadrimaculata* Panzer, 1798. The tree-based identification suggested that *A. onosmarum* was sister to a clade containing *A. balneorum* and *A. nigrovittata*. These results confirm that the obtained barcode is distinct from all other species represented on BOLD, and tentatively suggest phylogenetic affinities with *A. balneorum* and *A. nigrovittata*.

Behavioural observations and general remarks. A single male of *A. onosmarum* was captured in south-western Bulgaria (Blagoevgrad, Gorno Spanchevo) visiting *Onosma* sp. (given the challenging nature of *Onosma* identification, it was not possible to confidently

determine to species level; Teppner 1991) growing on piles of discarded building materials mixed with soil on 22nd May 2024. The surrounding habitat was composed of a small area of dry exposed slopes adjacent to a mountain road surrounded by deciduous woodland; *Onosma* was observed only on the refuse piles. Despite remaining at the site for several hours, no further individuals of *A. onosmarum* were seen.

On 13 June 2024 several individuals (approximately 10 males and five females) of *A. onosmarum* were observed in northern Greece (1.6 km E of Vatochori) on dry slopes with abundant *Onosma* sp. (Figs 11, 12). The individual *Onosma* plants formed spaced clumps, and male *A. onosmarum* were patrolling between clumps (Fig. 13), stopping only occasionally for nectar (Figs 14–16). Males were extremely active and difficult to photograph. Some males stopped to rest by finding thin upstanding stems of dead or dry vegetation and gripping them with their jaws. Males were not observed landing on the ground; presumably this would require more energy to return to the air, or it would increase the time taken to become airborne and therefore reduce their ability to quickly react to a passing female.

Females showed a similar behaviour, rapidly moving between *Onosma* clumps, usually with their tongue extended (Fig. 17). Upon encountering a flower, the females hang upside down from the corolla, using their long tongue to access the nectaries (Fig. 18). Females were also observed tightly gripping the corolla (whilst also keeping their tongue inside, Fig. 19) and were heard



Figures 11–12. 11. *Anthophora onosmarum* Morawitz, 1876 habitat in northern Greece on 13th June 2016; 12. *Onosma* sp. (Boraginaceae).



Figures 13–16. *Anthophora onosmarum* Morawitz, 1876 male behaviour visiting *Onosma* sp. (Boraginaceae) flowers.



Figures 17–20. *Anthophora onosmarum* Morawitz, 1876 female behaviour visiting *Onosma* sp. (Boraginaceae) flowers.

to emit a short high pitched buzz. This buzz released pollen which could be observed falling onto the underside of the metasoma as the bee released its grip on the corolla (Fig. 20). This pollen is presumably then groomed into the hind tibial scopa during flight.

Based on the long tongue (necessary to reach the deep nectaries of the *Onosma* flowers), the flower-buzzing behaviour, and the generally strong behavioural association with this plant genus (also mentioned in Morawitz 1876), we consider *A. onosmarum* likely to be narrowly oligolectic on this plant genus. It is not impossible that other genera of Boraginaceae are used; evidence from other bee groups is mixed. *Osmia* (*Osmia*) *apicata* Smith, 1853 (Megachilidae) is broadly oligolectic on Boraginaceae with a preference for *Onosma* (Haider et al. 2013), but this species does not buzz the flowers and scrapes out the pollen with its forelegs (Gogala and Surina 2011). *Hoplitis* (*Hoplitis*) *onosmaevae* Aubert, 2024 (Megachilidae) and *E. breviceps* however do buzz flowers of *Onosma* (Aubert et al. 2024a, 2024b), and seem to be narrow oligoleges of *Onosma*. In the new world, Boraginaceae-associated *Perdita* species (Andrenidae) also show variation within their use of this botanical family, from broad to very narrow specialisation (Portman et al. 2016). Ultimately, pollen analysis on collected specimens or more extensive behavioural observations would be needed to decisively conclude on this question.

Based on the examined specimens, collected males outnumber collected females by slightly more than 2:1 (21 examined males, nine examined females), and the flight period ranges from 22nd May to 13th July, with a median date of 16th June. This would fit with our observation on 13th June 2024 in northern Greece, where we observed a mixture of patrolling males showing signs of wear, combined with pollen collecting females, implying that nest provisioning was well underway.

Whilst *A. onosmarum* is here newly reported for Bulgaria, Greece, and Europe as a whole, inspection of specimens from the Borek Tkalcû collection (OÖLM) revealed that an undetermined male was actually collected in Bulgaria as early as 1987. Searches in the IBER collection in Sofia in 2023 and 2024 (TJW) did not uncover any further specimens, but searches were not exhaustive.

Distribution. Greece*, Bulgaria*, Turkey*, Georgia, Iran (Rasmont 2014; Ascher and Pickering 2024) (Fig. 21).

Distributional notes. The *locus typicus* is “Azchur” which is probably the village of Atskuri in southern Georgia (41.73°N, 43.16°E) and which is alternatively spelt “Azkur” or “Ahiska”. This village is located at an altitude of 900 metres above sea level. Iran is listed based on a GBIF record from the Donald Baker collection from the Snow Entomological Collection at the University of Kansas. Its details are “Iran: centr. Alborz, Kandavan Pass,

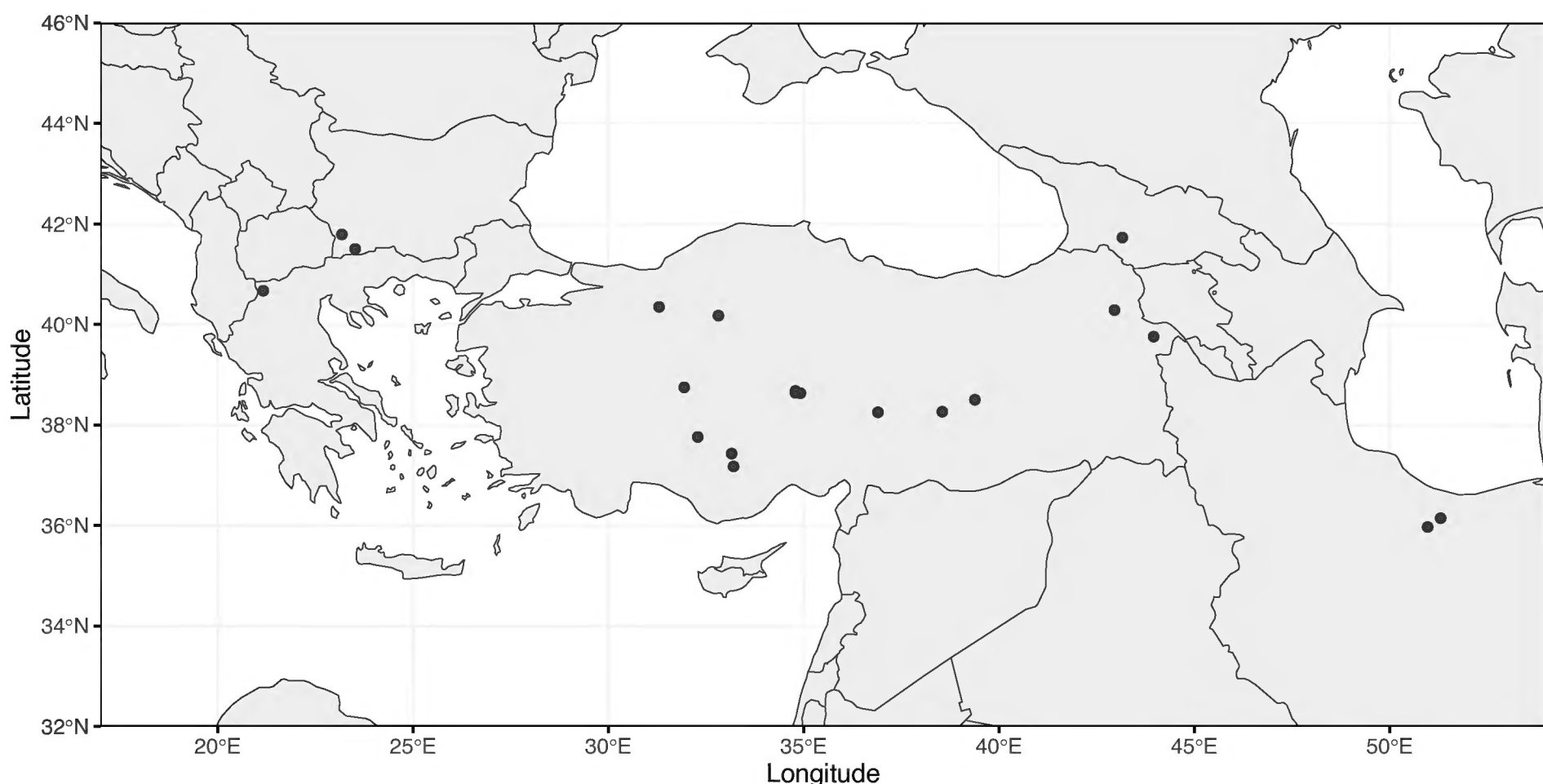


Figure 21. Distribution map for *Anthophora onosmarum* Morawitz, 1876 (green points) based on examined specimens and verified literature records.

nr. Pol-e-Zanguleh, 2200 m. 8 VII 1967. STA 8. Baker Exp.”. This record comes from just 40 kilometres to the north-east of the specimen we report here from north of Karaj. Rasmont (2014) also lists southern Russia (North Caucasus) which is plausible (although the species is not listed from Russia by either Levchenko et al. 2017 or Proshchalykin et al. 2023), and Libya, this being not at all plausible clearly the result of an encoding or other type of data error. We therefore take a conservative approach in our distributional listing based on confirmed specimens. Given the collecting locality in north-western Greece, *A. onosmarum* is almost certainly present also in Albania and North Macedonia. Where altitude data are available, *A. onosmarum* is found between 420–2200 metres above sea level, with 7/10 records with altitude information reported above 1000 metres above sea level.

Concluding remarks

Although the attractiveness of the plant genus *Onosma* for bees has been known for some time (Dukas and Dafni 1990; Teppner 1995; see also Teppner 2011), the recent finding of a newly described species (*Hoplitis onosmaevae*) ranging from southern France to Turkey and northern Iraq (Aubert et al. 2024b) and a new eucerine bee reported for western Europe (*Eucera breviceps*; Aubert et al. 2024a), as well as our observations of *A. onosmarum*, suggest that bees associated with this plant are still poorly investigated. Our findings in Greece indicate very local or sporadic appearance, given the abundance of their host plants. Similarly, we observed *Eucera breviceps* at only a single site (2 km E of Komnina, 40.5882°N. 21.8007°E), where three females were spotted on the same patch of

Onosma, even though *Onosma* was abundant at that site. Given the large body size of *A. onosmarum*, its overlooked presence in Europe is surprising, even with these stated caveats.

Overall, our limited observations correspond to those made by Teppner (1995), with *Osmia apicata* the dominant visitor to *Onosma* in the Balkans, with other species like *E. breviceps* only recorded once. Teppner (1995) also mentions an unidentified species of *Anthophora* collected on *Onosma* on the foothills of Mount Orvilos on the Greek/Bulgarian border (also known as Slavyanka), which could belong to *A. onosmarum* as it is less than 20 km from the known specimen collected from Gorno Spanchevo in Bulgaria. Taken together, these observations emphasise the rarity of both *A. onosmarum* and *E. breviceps* in the Balkans, in spite of the wide distribution and abundance of their host-plants. They also emphasise the growing trend of bee species with more Caucasian, Anatolian, or even Middle Eastern distributions occurring in under-surveyed mountainous parts of the Southern Balkans (Ghisbain et al. 2023; Aubert et al. 2024a, 2024b).

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References

- Ascher JS, Pickering J (2024). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). https://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed 21 Sep. 2024]
- Aubert M, Bonifacino M, Genoud D, Leclercq V, Schatz B (2024a) First observations of *Eucera (Cubitalia) breviceps* (Friese, 1911) (Hymenoptera: Anthophila: Apidae) in Italy and France, with updated information on the distribution and ecology of the species. *Osmia* 12: 5–18. <https://doi.org/10.47446/OSMIA12.2>
- Aubert M, Müller A, Praz CJ (2024b) A new osmiine bee with a spectacular geographic disjunction: *Hoplitis (Hoplitis) onosmaevae* sp. nov. (Hymenoptera, Anthophila, Megachilidae). *Alpine Entomology* 8: 65–79. <https://doi.org/10.3897/alpento.8.118039>
- Brooks RW (1983) Systematics and Bionomics of *Anthophora*: The *bomboides* Group and Species Group of the New World (Hymenoptera: Apoidea, Anthophoridae). University of California Publications in Entomology 98: 1–86.
- Brooks RW (1988) Systematics and phylogeny of the Anthophorine bees (Hymenoptera Anthophoridae; Anthophorini). The University of Kansas Bulletin 53(9): 436–575.
- Dukas R, Dafni A (1990) Buzz-pollination in three nectariferous Boraginaceae and possible evolution of buzz-pollinated flowers. *Plant Systematics and Evolution* 169: 65–68. <https://doi.org/10.1007/BF00935985>
- Ebmer AW (2021) Abweichende Datierungen der von Ferdinand Morawitz beschriebenen Bienenarten (Insecta: Hymenoptera: Apoidea) durch Vorausdrucke. *Annalen des Naturhistorischen Museums in Wien, Serie B* 123: 277–294.
- Friese H (1897) Die Bienen Europa's (Apidae europaeae). Theil III. Solitäre Apiden. Genus *Podalirius*. Friedländer & Sohn, Berlin, 316 pp.
- Ghisbain G, Rosa P, Bogusch P, Flaminio S, Le Divelec R, Dorchin A, Kasperek M, Kuhlmann M, Litman J, Mignot M, Müller A, Praz C, Radchenko VG, Rasmont P, Risch S, Roberts SPM, Smit J, Wood TJ, Michez D, Reverté S (2023) The new annotated checklist of the wild bees of Europe (Hymenoptera: Anthophila). *Zootaxa* 5327: 1–147. <https://doi.org/10.11646/zootaxa.5327.1.1>
- Gogala A, Surina B (2011) Foraging behaviour of the Bee *Osmia apicata* Smith, 1853 (Hymenoptera: Megachilidae). *Acta Entomologica Slovenica* 19(2): 139–144.
- Haider M, Dorn S, Sedivy C, Müller A (2013) Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees. *Biological Journal of the Linnean Society* 111(1): 78–91. <https://doi.org/10.1111/bij.12186>
- Levchenko TV, Byvaltsev AM, Proshchalykin MYu (2017) Family Apidae. In: Lelej AS, Proshchalykin MYu, Loktionov VM (Eds) Annotated Catalogue of the Hymenoptera of Russia. Volume I. Symphyta and Apocrita: Aculeata. Proceedings of the Zoological Institute Russian Academy of Sciences Supplement 6: 309–332.
- Marikovskaya TP (2000) The type specimens of species of the genus *Anthophora* Latreille, s. 1. (Hymenoptera, Apoidea) at the collection of the Zoological Institute of the Russian Academy of Sciences. *Tethys Entomological Research* 2: 205–210. [in Russian]
- Michener CD (2007) The Bees of the World, Second edition. The Johns Hopkins University Press, Baltimore, 953 pp.
- Morawitz F (1876) Zur Bienenfauna der Caucasusländer. *Horae Societatis Entomologicae Rossicae* 12: 3–69.
- Portman ZM, Neff JL, Griswold T (2016) Taxonomic revision of *Perdita* subgenus *Heteroperdita* Timberlake (Hymenoptera: Andrenidae), with descriptions of two ant-like males. *Zootaxa* 4214: 1–97. <https://doi.org/10.11646/zootaxa.4214.1.1>
- Praz C, Genoud D, Vaucher K, Bénon D, Monks J, Wood TJ (2022) Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation. *Journal of Hymenoptera Research* 91: 375–428. <https://doi.org/10.3897/jhr.91.82761>
- Proshchalykin MYu, Fateryga AV, Astafurova YV (2023) Corrections and additions to the catalogue of the bees (Hymenoptera, Anthophila) of Russia. *Zookeys* 1187: 301–339. <https://doi.org/10.3897/zookeys.1187.113240>
- Rasmont P (2014) Atlas of the European Bees: genus *Anthophora*. 1st Edition. STEP Project, Atlas Hymenoptera, Mons, Gembloux. <http://www.atlashymenoptera.net/page.aspx?ID=260>
- Rasmont P, Wood TJ (2024) An enigmatic Anthophorine bee from the south of France revealed as a new species: *Anthophora (Paramegilla) ahlmae* n. sp. (Hymenoptera: Apidae). *Annales de la Société entomologique de France (N.S.)* 60(2): 151–165. <https://doi.org/10.1080/00379271.2024.2325688>
- Teppner H (1991) 4. *Onosma* L. In: Strid A, Tan K (Eds) Mountain flora of Greece. Volume Two. Edinburgh University Press, 26–39.
- Teppner H (1995) Blüten und Blütenbesucher bei *Onosma* (Boraginaceae - Lithospermeae). *Feddes Repertorium* 106(5–8): 525–532. <https://doi.org/10.1002/fedr.19961060522>
- Teppner H (2011) Flowers of Boraginaceae (*Symphytum*, *Onosma*, *Cerithe*) and *Andrena symphyti* (Hymenoptera-Andrenidae): Morphology, pollen portioning, vibratory pollen collection, nectar robbing. *Phyton* 50(2): 145–180.